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A REVIEW

Phosphorus acqisition by rice

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Phosphorus (P) deficiency is one of the of the most important nutritional constraints to rice growth across the globe. The desire to improve the P acquisition efficiency of rice arises because of very low use efficiency of fertilizers and also are not always adequate to overcome the crop production constraints. Fertilizers are a costly input, such that their use limits the profitability of rice farming for high-input or low-input systems and the use of fertilizers for these two rice nutrients is inefficient. Rice-growing environments can be categorized into two very broad categories: 'upland' and 'lowland'. For the purposes of this review, we have explored whether there are other ways by which P acquisition by rice can be emphasized. Also, recent interests in foliar nutrition in rice, we must explore some of the other no traditional ways by which external application of P have been utilized. In this brief review paper, we have also tried to review some of the genotypes which are very efficient in low P tolerance.

Key words : Phosphorus acqisition, Rice

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INTRODUCTION

Phosphorus is one of the most limiting nutrients for plant growth in soil. Both acid and alkali soils are P deficient. P deficiency is perhaps one of the most important factors that limit plant yields on many soils. Its availability depends on soil characteristics and contents of labile P fraction. It is estimated that P availability to plant roots is limited in two thirds of the cultivated soil in the world (Baskar *et al*., 2000). Mineral nutrition in rice requires 16 essential elements, of which nitrogen (N), phosphorus (P) and potassium (K) are applied to rice fields as chemical fertilizers in large quantities. Nitrogen and P are fundamental to crop development because they form the basic component of many organic molecules, nucleic acids and proteins. Among these, phosphorus is from non-renewable natural resource and there is growing concern that the natural reserves of rock phosphate, the source of P fertilizer, are limited. A recent study conducted by the International Fertilizer Development Centre concluded that currently known and easily accessible world rock phosphate reserves will last for approximately another 300–400 years. P is an important component of nutrient supply chain that ensures potential yield realization of rice as it plays a crucial role in energy storage and transfer within cells, speeds up root development, facilitates greater N uptake and results in higher grain protein yields. Nutrient use efficiency has been widely used as a measure of capacity of a plant to acquire and utilize nutrient for biological and grain yield. The overwhelming majority of soils in the rice-producing areas are P-deficient with a high P-fixing capacity. In acidic soils free iron and aluminium oxides bind native and applied P into forms unavailable to plants, whereas in calcareous soils the abundant calcium and magnesium compounds bind inorganic phosphates into forms highly unavailable to plants. The high P-fixing capacity in both types of soils results in very low P-availability and thus, low rates of uptake by the plants. Thus, improving the uptake efficiency of the rice plant in P-fixing soils need to be a major research target.

P in soil :

In many agricultural systems in which the application of P to the soil is necessary to ensure plant productivity, the recovery of applied P by crop plants in a growing season is very low, because in the soil more immobile and unavailable for plant uptake because of adsorption, precipitation, or conversion to the organic form (Rajendran, 1984). Soil P is found in different pools, such as organic and mineral P. It is important to emphasize that 20 to 80 per cent of P in soils is found in the organic form, of which phytic acid (inositol hexaphosphate) is usually a major component (Rajendran, 1984). The remainder is found in the inorganic fraction containing 170 mineral forms of P (Hedley and McLaughlin, 2005). Soil microbes release immobile forms of P to the soil solution and are also responsible for the immobilization of P. The low availability of P in the bulk soil limits plant uptake. More soluble minerals such as K move through the soil via bulk flow and diffusion, but P is moved mainly by diffusion. Since the rate of diffusion of P is slow (10212 to 10215 m2 s21), high plant uptake rates create a zone around the root that is depleted of P.

Pi uptake across the plasma membrane and tonoplast :

The form of P most readily accessed by plants is Pi, the concentration of which rarely exceeds 10 mm in soil solutions (Bouma, 1969). The form in which Pi exists in solution changes according to pH. The pKs for the dissociation of H_3PO_4 into H_2PO_4 2 and then into HPO_4 22 are 2.1 and 7.2, respectively. Therefore, below pH 6.0, most Pi will be present as the monovalent H_2PO_4 2 species, whereas H_3PO_4 and HPO_4 22 will be present only in minor proportions. Most studies on the pH dependence of Pi uptake in higher plants have found that uptake rates are highest between pH 5.0 and 6.0, where H_2PO_4 2 dominates (Ullrich-Eberius *et al.*, 1984), which suggests that Pi is taken up as the monovalent form. Under normal physiological conditions there is a requirement for energized transport of Pi across the plasma membrane from the soil to the plant because of the relatively high concentration of Pi in the cytoplasm and the negative membrane potential that is characteristic of plant cells. This energy requirement for Pi uptake is demonstrated by the effects of metabolic inhibitors, which rapidly reduce Pi uptake. The precise mechanics of membrane transport are still not clear, although cotransport of Pi with one or more protons is the favored option based on the following observations.

P Translocation in whole plant :

Phosphorus (P) is a structural component of nucleic acids and is responsible for energy transfer, which is accomplished by phosphate ester and energy rich phosphate (Glass *et al.*, 1980). If the level of available P in soil is not adequate for optimum crop growth, phosphate fertilizers must be used to ensure that there are adequate amounts of this nutrient in the solution phase, which is usually variable and unpredictable (Chen and Barber, 1990). The formation of insoluble aluminium and iron phosphate compounds due to soil chemical reactions limits the plant-available P, making phosphate fertilization use efficiency by crops very low.

Organic anions may behave as ligands, chelating the metallic cations responsible for fixing phosphate (*i.e.*, Ca, Al, Fe), or the anions may desorbs phosphate from the sorbing surfaces of soil constituents. Efficiency for chelation varies according to the number and position of the hydroxyl groups on the anion and the metal cation, and is more efficient when 5- or 6-ring metal–anion structures can be developed.

Mycorrhizae in P uptake :

There is a general perception that Pi uptake by plants occurs as a direct consequence of uptake from the soil by root cells. However, in more than 90 per cent of land plants, symbiotic associations are formed with mycorrhizal fungi. In these plants the fungal hyphae play an important role in the acquisition of P for the plant (Bolan, 1991). Mycorrhizae can be divided into two main categories: ectomycorrhizae and endomycorrhizae, of which vesicular arbuscular mycorrhizae are the most widespread in the plant kingdom. The mycorrhizal symbiosis is founded on the mutualistic exchange of C from the plant in return for P and other mineral nutrients from the fungus. Influx of P in roots colonized by mycorrhizal fungi can be 3 to 5 times higher than in nonmycorrhizal roots.

The few published studies of the kinetics of Pi uptake indicate that mycorrhizal roots and isolated hyphae have P-uptake systems with characteristics similar to those found in nonmycorrhizal roots and other fungi (Smith and Read, 1997). Germ tubes of the vesicular arbuscular mycorrhizal fungus *Gigaspora margarita* have two Pi-uptake systems (Km 2–3 mm and 10,000–11,000 mm) (Thomson and Beveridge,1993). A recent molecular study (Harrison and van Buuren, 1995) identified the gene *GvPT*, which encodes a high-affinity fungal phosphate transporter (Km 5 18 mm) in external hyphae that is similar in both structure and function to high-affinity transporters in plants. A number of factors may contribute to the increased rate of Pi uptake measured in mycorrhizal plants (Smith and Read, 1997). An extensive network of hyphae extends from the root, enabling the plant to explore a greater volume of soil, thereby overcoming limitations imposed by the slow diffusion of Pi in the soil. Several studies have shown that the depletion zone around plant roots, which is caused by plant uptake and the immobile nature of Pi, is larger in mycorrhizal than in nonmycorrhizal plants (Bolan, 1991). Mycorrhizal fungi may also be able to scavenge Pi from the soil solution more effectively than other soil fungi because C (which may be limiting in the soil) is provided to the fungus by the plant. The plant/fungus association could, therefore, enable the plant to compete more effectively with soil micro-organisms for the limited amount of available soil Pi. Mycorrhizal fungi may also be able to acquire P from organic sources that are not available directly to the plant (e.g. phytic acid and nucleic acids) (Jayachandran *et al*.,1992).

External P application on growth, quality and yield attributes :

Soil-applied fertilisers react in soils containing high levels of aluminium, calcium and iron to form insoluble compounds which limit the effectiveness of soil-applied phosphorus (P) fertilisation strategies (Hedley and McLaughlin, 2005).

Baskar *et al*. (2000) revealed that the growth parameters yield attributes, yields and benefit cost ratio increased significantly with application of 40 kg P_2O_5, 40 kg S and 5 kg Zn/ha. He further revealed that the yield of wheat and protein increased significantly in the grain and straw of wheat with the increasing levels of phosphorus and zinc in the soil. They also reported that the application of 5 tonnes of vermicompost/ha significantly increased grain, straw yields and harvest index of wheat over no vermicompost application. Application of 100 per cent recommended dose of N, P recorded significantly higher grain and straw yields and harvest index of wheat than the lower levels of N and P. Highest grain and straw yields and harvest index were recorded with inoculation of *Azotobacter* and PSB which was closely followed by *Azotobacter* inoculation. Maximum gross and net return/rupees of investment were obtained with vermicompost application of 5 t/ha, 100 per cent N, P and dual inoculation of *Azotobacter* and PSB among the levels of vermicompost, N, P and biofertilizers, respectively.

Sathyamoorthi *et al*. (2007) reported that he conjunctive use of vermicompost, phosphate solubilizing bacteria (PSB) and zinc (Zn) in collaboration with 100 per cent recommended fertilizer dose produced significantly higher grain and straw yields of wheat compared to its counterpart of 50 per cent NPK, whether applied alone or in combination with farm yard manure (FYM), PSB, Zn and vermicompost. The yield attributes, such as earhead length (cm), number of grains per earhead and 1000-grain weight (g) increased by increasing fertilitiy levels from 50 to 100 per cent. In economic consideration, it was found that integration of FYM/vermicompost and Zn and PSB with 100 per cent recommended NPK gave higher net income/ha (Rs. 32294) and B:C ratio (2.00) compared to the 50 per cent recommended NPK.

Water stress and foliar phosphorus uptake :

Low soil moisture limits root access to P, as P needs to be in solution for uptake (Dos Santos *et al*., 2004). While water may still be available in the subsoil, mineral nutrition can become the growth-limiting factor as nutrients are often stratified in the dry topsoil. Foliar work by Alston (1979) investigated the effects of soil water content and foliar fertilisation of N and P on wheat yield. The P was applied at a rate of 9–18 mg pot^{-1} as H_3PO_4, where 15 mg pot^{-1} is equivalent to 10 kg ha^{-1}). A grain yield increase was documented for plants with foliar applications although Alston (1979) attributed the response to the N applied. Alston (1979) commented that increasing grain yield after head emergence can be achieved by keeping the soil wet to enable nutrient uptake or by applying foliar fertiliser directly to the plant.

Data from Mosali *et al.* (2006) also suggested increases in grain yield that resulted from foliar P application, generally took place in seasons of water stress. This is likely due to reduced root soil contact for nutrient exchange enhancing the benefits of foliar P in lower rainfall areas and/or years. The application of foliar nutrients under water stress conditions requires careful consideration of stomatal opening and rate of fertiliser drying on the leaf before penetration is possible.

Leaf surface and leaf age :

It is accepted that the absorption rates of most mineral nutrients by young leaves are greater than those of old ones. Fisher and Walker (1955) also reported a higher P absorption by young apple leaves than that of old ones. Lower nutrient uptake by basal leaves was attributed to a decreased metabolic activity and/or a lower amount of ectodesmata on the surface of a leaf.

Nutritional status and plant development stage :

Leaf ability to take up mineral nutrients also is dependent on the nutritional status of a plant. Clarkson and Scattergood (1982) proved that the absorption rate of P by the leaves of P deficient barley (*Hordeum vulgare* L.). Plants were twice as high as that of plants well supplied with P via the roots. In addition, in P deficient plants much more P was translocated from the leaves, particularly to the roots.

Phosphorus foliar fertilization :

It is important to apply some P to the soil at the beginning of the crop growth cycle to provide essential P for early growth and, if a maintenance fertilisation strategy is required, to replace P exported in previous crops (Batten *et al.*, 1986). Foliar P can be applied directly to the plant and only when required and this potentially provides increased fertiliser use efficiency (Silbertstein and Wittwer,1951; Dixon, 2003 and Girma *et al.*, 2007). Field studies applying P after anthesis have resulted in more tiller dry matter but varying effects on P content in the grain and grain yield.When a plant progresses from the vegetative stage of growth to the reproductive stage of growth, photosynthate produced by the leaves is translocated to the developing seed, which has a higher P requirement (Gray, 1977; Batten *et al.*, 1986; Peng and Li, 2005). Applying foliar P in early growth stages can increase the number of fertile tillers (Elliott *et al.*, 1997 and Grant *et al.*, 2001).

Breeding rice for enhanced phosphorus use efficiency:

Phosphorus application is essential to minimize yield loss on the soil. However, most of the P applied to soil can be converted into unavailable forms that cannot be easily utilized by plants. With an increase in the price of P fertilizer and a growing concern about environmental pollution, screening, and cultivating, low-P tolerant cultivars have become a hot research field. Development of efficient genotypes with a great ability to grow and yield in P-deficient soil is, therefore, an important goal in plant breeding. Release of P efficient genotypes in both high- and low-input farming systems would reduce the production costs associated with P fertilizer applications, minimize environmental pollution and contribute to the maintenance of P resources globally. Plant species and genotypes of a given species develop diverse adaptive responses to P deficiency. To improve growth under P-deficient conditions, P-efficient plants have evolved two major mechanisms: (i) increasing P acquisition (root morphology, root exudation and P uptake mechanisms), and (ii) enhancing P utilization (internal mechanisms associated with conservable use of absorbed P at the cellular level).

The development of rice cultivars capable of using a higher portion of the fixed P already present in soils may be an attractive and cost effective approach to increasing rice yields where P deficiency is the major constraint. An integrated fertilization-plant breeding approach seems likely to give more economically viable and practical results in future. The possibility of selecting and breeding P efficient varieties has been stimulated by increased knowledge about P-uptake differences in crop plants and their cultivars. In order to achieve this, breeders have to work in close conjunction with disciplines like soil science, plant physiology and agronomy. It has been observed and reported invariably that modern day varieties irrespective of the crops are not tolerant to low input situations but respond well to external application. However, tolerance to low P is reported in landraces but they hardly respond to P application. Combining both low P tolerance and response to its application is necessary to develop cultivars for sustaining future production. Most of our breeding programmes particularly in rice are operating with the germplasms having very narrow genetic base. Elite varieties which are closely related are being used as parents and use of landraces possessing characters such as low P tolerance in addition to tolerance to other biotic and abiotic stresses is diminishing. There is substantial genetic variation in traits associated with PUE within the crop plants that have been reported by various workers. Analysis of this variation has led to the identification of numerous genetic loci that influence PUE. The ability to identify these quantitative trait loci (QTL) suggests that improvements in PUE may be gained through conventional or marker-assisted breeding programmes, directed gene identification and genetic engineering, or a combination of these approaches. One promising step toward developing more P-efficient cultivars was the identification of a major QTL named *Pup1*in the indica rice variety Kasalath, which accounted for ~ 80 per cent of the phenotypic variance for P-deficiency. The QTL has been transferred to the genetic background of Nipponbare, a variety which has low P uptake and the resulting near-isogenic line, (named NIL-C443), was genetically identical to Nipponbare by ~ 92 per cent. Interestingly, when grown on P limiting soils, NIL-C443had a threefold higher biomass than Nipponbare. This improvement in growth was due to the ability of the NIL to acquire more P from the soil. Higher root growth rates and more efficient P uptake per unit root size (uptake efficiency) were the main differences between NILC443 and Nipponbare. *Pup1* has been recently fine mapped on long arm of chromosome 12 of rice with the help of SSR markers. Four SSR markers RM28102, RM1261, RM277 and RM519 were observed to be very closely linked to *Pup1*. Now, it is established that *Pup1*-specificprotein kinase gene6, which is named phosphorus-starvationtolerance 1 (*PSTOL1*) acts as an enhancer of early root growth, thereby enabling plants to acquire more phosphorus and other nutrients. This offers the opportunity for marker assisted deployment of the gene(s) into the popular varieties sensitive to low P conditions. Efforts should also be intensified for identification of low P tolerant donors which are devoid of Pup1.

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